9-2018

Wild, native bees and managed honey bees benefit from similar agricultural land uses

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Published in *Agriculture, Ecosystems and Environment* 268 (2018), pp 162–170.
doi 10.1016/j.agee.2018.09.014

Submitted 15 January 2018; revised 14 August 2018; accepted 11 September 2018;
published 22 September 2018.

Wild, native bees and managed honey bees benefit from similar agricultural land uses

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Abstract

Although both managed and unmanaged bees are important pollinators of crops and wild plants, efforts to address questions about landscapes that best support pollinators often focus on either wild pollinators or honey bees. This study examined if there was concordance between the success of wild bee communities and managed honey bee colonies at sites varying in floral availability and disturbance level in a predominantly agricultural landscape. We also determined which agricultural land uses best supported wild bee communities. The study area in the state of North Dakota in Northern Great Plains in North America is home to understudied native bee communities as well as over ¼ of U.S. commercial honey bee colonies during the summer months. There is an assumption that honey bees can do well in agricultural areas but that wild bees need natural areas to thrive. We compared wild bee community success with health and survival of managed honey bees (data obtained from a related study) at six apiary locations over three years. We examined wild bee communities and surrounding land uses at 18 locations, three of which were spatially associated with each of six apiary locations. Wild bee abundance and species diversity were positively correlated with honey production, a measure of honey bee success, indicating that locations supporting successful honey bee colonies also supported successful wild bee communities. Grasslands, bee-forage crops, wooded areas, and wetlands were associated with increased abundance, species diversity, or functional diversity of wild bee communities. Crops not providing forage

for bees, predominantly soybean, corn, and wheat, were associated with decreased functional diversity, decreased aboveground nesting bees and bees with shorter active season durations, and decreased honey bee survival. Pollinator conservation efforts retaining and enhancing grasslands, wooded areas, wetlands, and crops providing bee forage will likely support the growth, reproduction, and survival of diverse wild bee communities and the success of managed honey bees in areas dominated by intensive agriculture.

Keywords: Agriculture, Land use, Apoidea, Wild bee, Native bee, Managed bee, *Apis mellifera,* Honey bee

1. Introduction

Both wild and managed bees rely on resources provided by the landscape within their foraging range. Because of this, the success of bees may be considered a reflection of the quality of their surrounding landscape. There is mounting evidence of decline in some wild bee populations (Biesmeijer et al., 2006; Burkle et al., 2013; Senapathi et al., 2015), while honey bees and beekeepers continue to be faced with numerous interacting factors such as parasites, nutrition, pesticides, and socioeconomics (Lee et al., 2015; vanEngelsdorp and Meixner, 2010). Efforts to address questions about landscapes that best support pollinators often focus on either wild pollinators (Hinners and Hjelmroos-Koski, 2009; Hopfenmüller et al., 2014; Loos et al., 2014; Lowenstein et al., 2012; Winfree et al., 2011) or honey bees (Couvillon et al., 2014; Gallant et al., 2014). However, large-scale land-use trends resulting in decreased forage and nesting habitat pose threats to all pollinators (Otto et al., 2018; Thogmartin et al., 2017; Wright and Wimberly, 2013). Such concerns about broadly-occurring pollinator population and health declines highlight the importance of identifying landscapes that contribute to the success of all bees, native and nonnative, wild and managed.

The Northern Great Plains (NGP) of North America is an important region for both managed and wild pollinators (Koh et al., 2016; Smart et al., 2016b) and is a major area of agricultural production (USDANASS, 2013) with 90% of private land in agricultural use (Rashford et al., 2011). North Dakota is the top honey producing state in the U.S. with approximately 485,000 honey bee colonies producing over 17 million kilograms of honey, valued at $70 million in 2016 (USDA-NASS, 2017). Many of these honey bee colonies are transported throughout the country for crop pollination in late winter and early spring. North Dakota is also home to many wild bees with historical records suggesting the presence of over 300 bee species (Stevens, 1948).

In recent years, agricultural land-use features and crops thought to be supportive to bees have decreased due to shifts toward row crops grown for biofuel production, raising concerns about the fate of associated effects on

pollinators (Gallant et al., 2014; Otto et al., 2016; Smart et al., 2016a). The decreasing land uses include semi-natural lands (Alaux et al., 2017; Hopfenmüller et al., 2014; Le Feon et al., 2010; Öckinger and Smith, 2006; Riedinger et al., 2015; Smart et al., 2016b; Sponsler and Johnson, 2015; Steffan-Dewenter et al., 2002; Westphal et al., 2003), crops providing bee forage (Ayers and Harman, 1992; Holzschuh et al., 2013; Riedinger et al., 2015; Rollin et al., 2013; Scheper et al., 2014; Westphal et al., 2003; Zou et al., 2017), wooded areas (Carré et al., 2009; Jha and Kremen, 2013; Morandin and Kremen, 2013; Moroń et al., 2014), and wetlands (Koh et al., 2016). Because of the pre-eminence of agriculture and the important role of pollinator habitat in the NGP, it is crucial to identify bee-utilized habitat within agricultural lands that provides broad support for both wild and managed bees, while also allowing for a productive agricultural economy. Maintaining and increasing acreage in land-use features supporting bees could help conserve wild bee communities and ensure the availability of honey bees for pollination service delivery throughout the country.

The objectives of this study were to determine if wild bees and managed honey bees were successful in the same landscapes and to describe how agricultural land use may best support wild bee communities. We addressed the following two questions: 1) Are wild bee community metrics (abundance, species richness, species diversity, and functional trait diversity) associated with honey bee metrics (honey production and colony survival)? and 2) What land-use types are associated with successful wild bee communities? Our study is timely and informative, providing evidence on how pollinator habitat management efforts may be prioritized in agricultural areas.

2. Methods

2.1. Study sites and land use quantification

We chose six apiary sites existing across an agriculture-grassland gradient based on GIS analysis of the areas surrounding each apiary site (Smart et al., 2016b). Wild bee survey locations were located between 1 and 2.5km of apiary sites. These survey locations were at least 1km from each other. The minimum distance of 1km from apiary sites and other wild bee survey locations was chosen to decrease potential foraging overlap (Fig. 1). We chose exact wild bee survey locations based on land access, the presence of floral resources on which to find foraging bees, and variability in the presence of potential wild bee habitat, such as wooded areas and grasslands (Table S1). Survey locations primarily occurred along roadside ditches where floral resources were predominantly located.

Methods for quantifying land use are detailed in Smart et al., 2016b. To summarize, land use was determined via visual observation and supplemented with data obtained from the National Agricultural Statistics Survey Cropland Data Layer (NASS CDL). Final quantification was done via GIS analysis (ArcGIS v.10), which provided the square meters of various land-use types within a 3.2km radius around each apiary site (Fig. 1). The distance of 3.2km was chosen as a realistic total area (approx. 32km2) over which honey bee colonies at a given site would be expected to forage (Beekman and Ratnieks, 2000; Visscher and Seeley, 1982). We grouped land uses into the following categories based on similarities in floral abundance and disturbance: wooded, wetlands, open water, grasslands, non-alfalfa hay-land, pasture, crops providing potential bee forage, crops not providing significant bee forage, and ruderal land (Table 1). Survey locations varied widely in the amount of land use in these categories (Table S1). Casual observations found no wild bee visitation and low frequency of honey bee visitation to soy and corn at all study sites so we grouped these crops with the other crops not providing bee forage (wheat and oats). This observation was corroborated by analysis of honey bee-collected pollen from apiaries at these study sites (Smart et al., 2016b).

We examined land use surrounding each wild bee survey location at scales of 1500m, 700m, and 300m (Fig. 1). These scales were chosen to encompass varying flight ranges for different groups of bees and their different uses of the surrounding landscape (Greenleaf et al., 2007; Steffan-Dewenter et al., 2002). At the 1500m scale some survey locations overlapped. However, we assumed this overlap did not bias observed relationships as the overlapping area was a small proportion of the total area examined and the majority of bees from collections at the central collection site would not be foraging near the edge of the 1500m buffer.

2.2. Wild bee community sampling and characterization

In 2010, we chose two wild bee survey locations near each of the six apiary sites, resulting in twelve bee survey locations. In 2011, we added an additional survey location around each apiary site to better encompass landscape variability, resulting in eighteen bee survey locations for 2011 and 2012. We sampled wild bees between May and September, once every three weeks in 2010, for a total of six sampling rounds per survey location, and once every four weeks in 2011 and 2012, for a total of five sampling rounds per survey location. Logistic constraints led to the compromise between the number of survey locations and sampling frequency, resulting in less frequent sampling at more sites in 2011 and 2012. We sampled all sites within three to four days during each sampling round using two different sampling methods: sweep netting and bowl traps. Although bowl traps are both efficient

and unbiased in terms of observer bias (Westphal et al., 2008), they have other potential biases (Jean, 2010). We included both sampling methods to maximize the number of species caught and to compensate for variable performance of each individual sampling method.

2.2.1. Sweep netting

We visited each survey location twice for sweep netting during each sampling round, with one sample between 10 a.m. and 1 p.m. and another between 1 p.m. and 6 p.m. Sampling took place when there was no precipitation and the temperature was greater than 15 °C. In 2010, we spent thirty minutes of sweep time, with two 15 min samples, at each survey location per sampling round with the survey effort focused on patches of blooming flowers. In 2011 and 2012, we reduced sampling time to twenty minutes per sampling round per site, due to the increase in survey location number. Sweep netting took place along a meandering transect with observers walking at a consistent pace while constantly sweeping through vegetation, covering approximately 100m2 in ten minutes with the transect path varying to encounter patches of blooming flowers. All bees were collected from sweep nets with the exception of honey bees and other readily-identifiable bees, primarily bumble bees, which were identified to species, counted, and released.

2.2.2. Bowl trapping

In 2010, we set up thirty-six bowl traps for approximately twentyfour hours at each survey location during each sampling round along two orthogonal lines when possible, or along one straight line, with 5m between bowls, along roadside ditches or other open areas. The traps consisted of 200ml plastic cups painted either fluorescent blue, fluorescent yellow, or white (Guerra Paint and Pigment, New York, NY) filled with a 2% soap solution (Dawn dish soap, Procter & Gamble, Cincinnati, OH) attached to bamboo stakes elevating the traps slightly above vegetation height to ensure visibility. Due to the increase in the number of survey locations in 2011 and 2012, the number of cups was reduced to twenty-four to enable timely sample processing.

2.2.3. Identification

We identified bees to species whenever possible using keys and comparisons with previously identified materials (Ascher and Pickering, 2015; Gibbs, 2010; Laberge, 1969; Mitchell, 1960). A subset of bees (5%) was sent to experts (Dr. John Ascher, Dr. Jason Gibbs, Mike Arduser, Sam Droege, Dr. Karen Wright, and Joel Gardner) for creation of a synoptic set, confirmation of identifications, and identification of groups for which there were no available keys. Ten bee types representing 15% of all specimens were identified to species groups or as cf. species, meaning the species was not well documented from that part of the continent or potentially represented

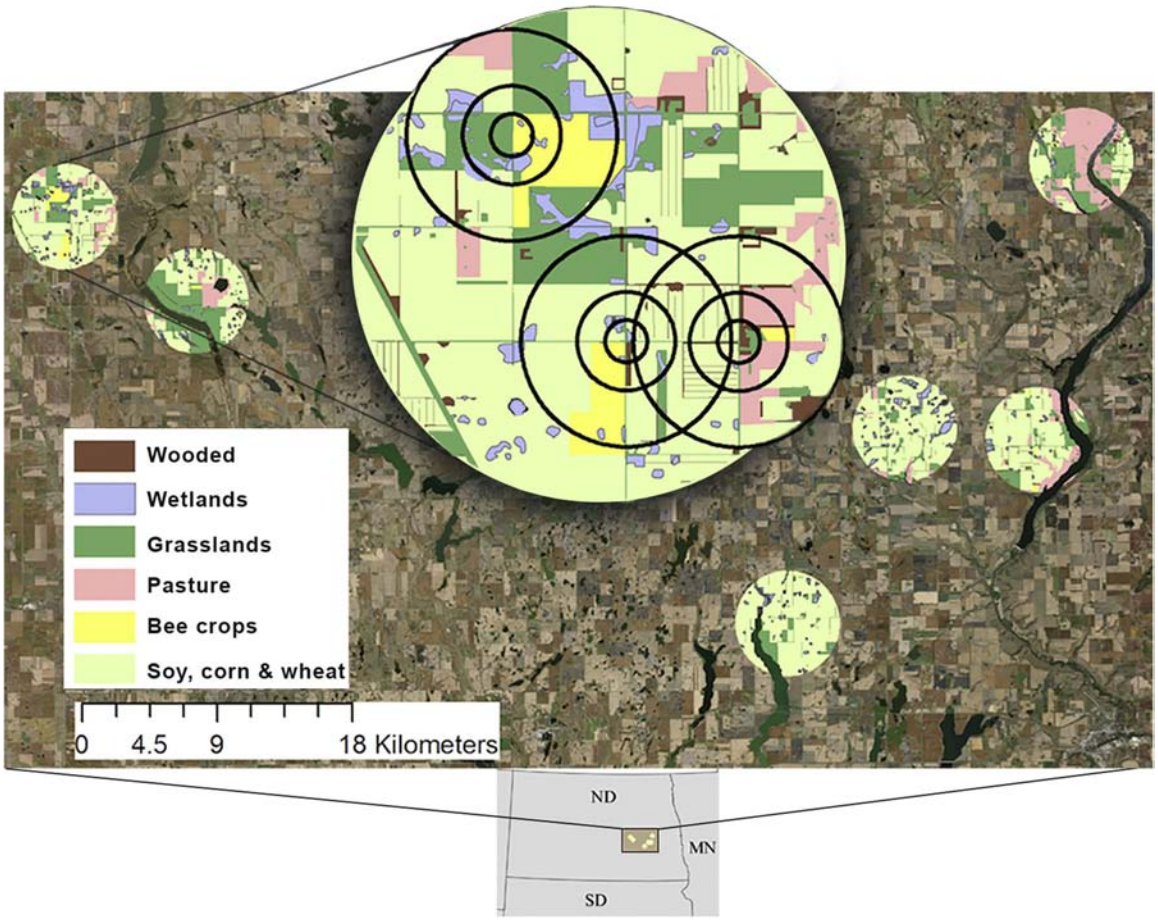

Fig. 1. Locations of six apiary sites housing wild bee survey locations in the Northern Great Plains in North Dakota. Land use was examined within 1500m, 700m, and 300m of survey locations as denoted by black circles. Wooded included flowering trees and shelterbelts. Wetlands included cattails and ephemeral wetlands. Grasslands included grasslands and Conservation Reserve Program land. Pasture included actively, or recently grazed lands. Bee crops included canola, sunflower, and alfalfa. Soy, corn & wheat included soy, corn, wheat, and oats.

undescribed species. Specimens are deposited in the University of Minnesota Insect Collection and the University of Minnesota Bee Lab. All records are databased and have been shared with DiscoverLife and the USGS Pollinator Library.

2.2.4. Community characterization

We characterized bee communities using measures of 1) abundance, 2) species richness, 3) effective species diversity, 4) functional trait diversity, and 5) community weighted means for individual functional traits to examine

Table 1. Land-use categories and the degree of disturbance, estimated floral cover, and total land cover within 3.2km of all six apiary sites. Land-use categories are followed by percentages of included land-uses. CRP=USDA Conservation Reserve Program.

Land-use category	*Disturbance*	*Floral cover*	*Cover*
Wooded: flowering trees (73%), shelter belts (27%)	Low	Low (< 0.01%)	2%
Wetlands: cattails (82%), ephemeral wetlands (18%)	Low	Low (< 0.01%)	5%
Open water	Low	Low (< 0.01%)	8%
Grasslands: grasslands (53%), CRP (47%)	Low	Moderate (3%)	11%
Hay land	Moderate	Moderate (3%)	4%
Pasture	Moderate	High (9%)	12%
Bee-forage crops: canola (45%), alfalfa (29%), sunflower (26%)	Moderate to high	High (56%)	1%
Soy, corn, & wheat: soy (56%), corn (22%), wheat (22%), oats (< 1%)	High	Low (< 0.01%)	55%
Ruderal land	Moderate to high	Low (< 1%)	3%

effects on particular functional groups. Measures were summarized over each year to examine the community as a whole, encompassing seasonal variability over each year. Bee abundance was the total number of bees collected at each survey location summarized over all sampling rounds each year. We quantified species richness using first-order jackknife estimation, a non-parametric estimator to control for the confounding effects of sampling effort due to potential bias and smaller sample sizes for estimates at each survey location and year (Walther and Morand, 1998) using the program EstimateS (Colwell, 2009). We quantified effective species diversity using the exponential Shannon's index of entropy in EstimateS version 9 (Colwell, 2009), a measure that examines the abundance of each bee species, the evenness of the community, and weights bee species by their frequency without disproportionately favoring either rare or common species (Jost, 2006).

We included functional traits to provide additional information about land use due to its differential effects on growth, reproduction, and survival of different functional groups (Cadotte et al., 2011; Violle et al., 2007). We chose to include the following traits because they are important descriptors of bee ecology and may predict bee community stability: nesting habit (Williams et al., 2010), duration of seasonal activity (De Palma et al., 2015), floral specialization (Grundel et al., 2010; Weiner et al., 2014), and tongue length (Goulson et al., 2008). We determined trait qualities from examination of specimens from this study as well as from previously published information (Table 2, Table S2). We measured functional dispersion,

Table 2. Traits used to assess functional diversity of bee communities. Active season length is the number of months during which adults were active. Floral specialization was categorized as polylectic, visiting a wide variety of floral hosts, or oligolectic, visiting a limited range of floral hosts. Tongue length was the combined length of the tongue, glossa, and prementum.

Functional trait	Categories or unit of measure	Data source	Percent of total abundance for categorical traits or mean ± standard deviation for continuous traits
Nesting habit	Below-ground, above-ground, cleptoparasitic	Hobbs, 1968, 1967, 1966; Michener, 2000; Sheffield et al., 2008	Below 77%, Above 22%, Cleptoparasitic 1%
Active season length	Number of months	2010–2012 collections and historical collections	3.3 months±1.6 months
Floral specialization	Polylectic, oligolectic	Hurd et al., 1980; Robertson, 1926; Wolf and Ascher, 2008	Polylectic 78%, Oligolectic 22%
Tongue length	Combined length of tongue, glossa, and prementum	Based on inter-tegular distances of 2010–2012 collections using BeeIT package (Cariveau et al., 2016)	2.8mm ± 1.8mm

an abundance-weighted measure of functional trait diversity that is unaffected by species richness and is less sensitive to species with extreme trait values using the FD package (Laliberté and Legendre, 2010) in R version 3.2.1 (R Core Team, 2015). We applied a correction on the species-by-species functional distance matrix to ensure it was Euclidean (Cailliez, 1983). In addition to functional dispersion which summarizes over a suite of traits, community weighted means, the average of trait values weighted by the relative abundances of each species (Lavorel et al., 2008; Ricotta and Moretti, 2011), were calculated for individual functional traits using R package FD (Laliberté and Legendre, 2010). Although cleptoparasitism is suggested as a good monitor of bee community health (Sheffield et al., 2013), the low frequency among the bees in this study (1%) prevented inclusion as a response variable.

2.3. Data analysis: comparing honey bee and wild bee success

For comparison of relative success of honey bees and wild bees, data for all wild bee survey locations within 3.2km of each apiary site were grouped (2010: n=2, 2011-12: n=3). Summary measures of wild bee success

(abundance, species richness, species diversity, and functional diversity) were calculated for wild bees surveyed at each apiary site each year. The relationship between measures of wild bee success and honey bee success from Smart et al. (2016b) (average honey production and overall proportion of surviving honey bee colonies) was assessed using Pearson's correlation coefficient (r) with R package Hmisc (Harrell, 2015).

2.4. Data analysis: land-use effects on wild bee communities

We examined the relationships of bee community measures to landuse categories using mixed-effects multiple linear regression models with bee community measures as the response variables, land use and years as fixed effects, and survey location nested within site as a random effect. We excluded bowl trap data from analyses of bee community measures that included abundance (all measures except species richness) due to possible bias from an interaction between floral cover and performance of bee collection method. We examined diagnostic plots to ensure homoscedasticity and normality of errors. To avoid collinearity of covariates, we removed predictors with variance inflation factors greater than three from models (Zuur et al., 2010). Transformations, error distributions, and covariates removed due to collinearity are summarized in Table S3. We standardized regression predictors as z-scores using R package arm version 1.8–6 (Gelman and Su, 2015) to permit comparison among regression coefficients. We obtained conditional and marginal R^2 values by running models with restricted maximum likelihood and obtained the pseudo-R^2 for generalized mixed-effect models using R-package MuMIn (Bartoń, 2015).

2.5. Data analysis: land-use effects on honey bees

Smart et al. (2016b) examined the relationship of measures of honey bee success to the following land uses: (1) semi-natural land, (2) potential bee-forage cropland, and (3) wetlands. One additional land use category (crops not providing bee forage) was included here by using a simple linear mixed effects model using lme4 (Bates et al., 2015). This analysis allowed us to examine the relationship between the predictor (area of land use in soy, corn, wheat and other small grain crops (logtransformed m2)) and two responses: (1) annual apiary survival (number of colonies surviving out of 24 at each apiary and year); and (2) apiary honey production (mean kg per year) with apiary and year specified as random effects as per Smart et al. (2016b).

3. Results

3.1. Community composition

Sweep net and bowl trap collections together yielded 13,426 bees representing 149 species, morpho-species, or species groups. This represented approximately 75% of the estimated minimum bee species number in the study area (Jack 1 estimation). Most bees were groundnesting (72% of species, 82% of individuals), polylectic (70% of species, 82% of individuals), and had tongue-lengths less than 2.5mm (60% of species, 70% of individuals) (Table S2). Sweep net collections yielded 2028 bees, representing 117 species, morphospecies, or species groups. Bees collected with sweep nets represented approximately 60% of the estimated minimum number of bee species in the study area (Jack 1 estimation). Of bees collected using only sweep nets, most were groundnesting (73% of species, 77% of individuals), polylectic (69% of species, 78% of individuals), and tongue-lengths less than 2.5mm (50% of species, 67% of individuals) (Table S2).

3.2. Comparison of honey bee and wild bee success metrics

Wild bee community success was positively associated with honey bee success. Wild bee abundance and species diversity were positively correlated with annual honey production (Fig. 2, Table 3). Honey bee colony survival was not correlated with any of the wild bee success measures.

3.3. Land use associations with wild bee communities

Several agricultural land uses had positive associations with wild bee community success (Figs. 3 and 4, Tables S4, S5). Semi-natural land uses (wooded areas, wetlands, and grasslands) and some managed land uses (crops providing bee forage and pastures) were associated with higher wild bee community metrics at varying scales. Some wild bee community metrics had negative associations with soy, corn, wheat and other small grain crops.

3.4. Honey bee success negatively related to soy, corn, wheat and other small grain crops

This study expanded on the examination of associations between land use and honey bee success of Smart et al. (2016b) by examining associations between soy, corn, wheat and other small grain crops and honey bee success measures. We demonstrate a significant negative association between these crops, which do not provide forage for bees, and honey bee colony survival at

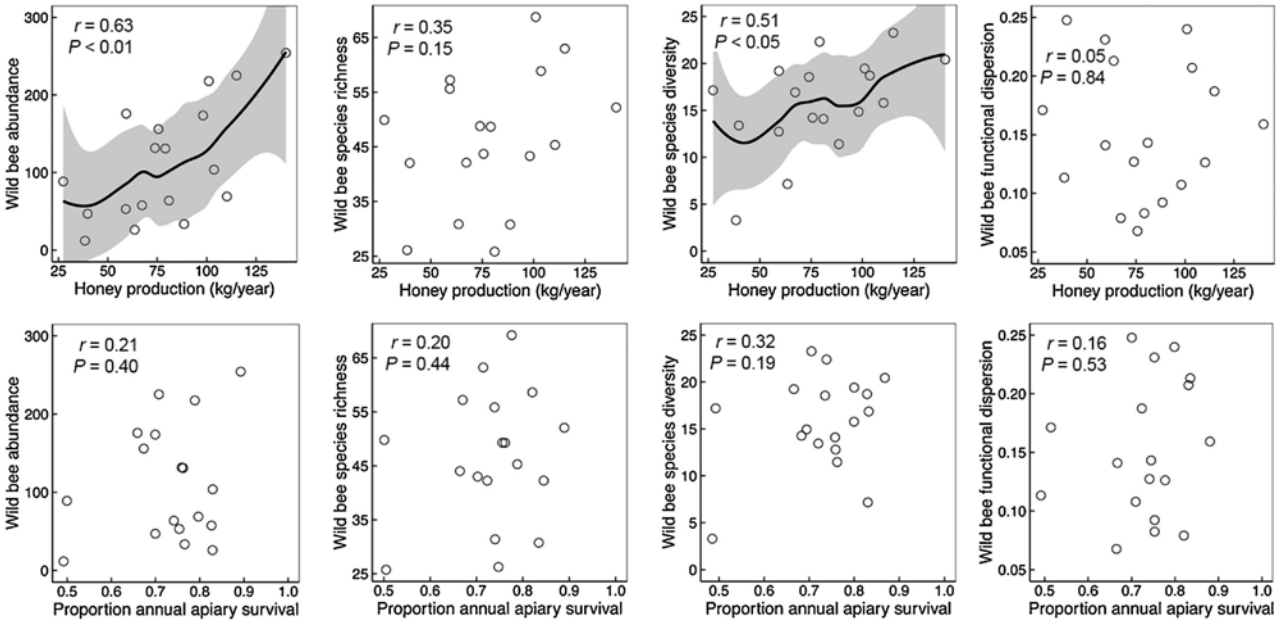

Fig. 2. Correlation between wild bee and honey bee success measures. A LOESS smoother was used to draw regression lines to aid visual interpretation.

Table 3. Bee success at six study sites. Survival represents the proportion of annual honey bee colony survival. Honey represents the average annual kgs of honey production at six apiary sites. exp*H* represents the exponential Shannon index. *FDis* represents the functional dispersion index. Honey bee measures are from Smart et al. (2016b).

		Honey bee success		Wild bee success			
Site	Year	Survival	Honey (kgs)	Abundance	Species richness	exp*H*□	*FDis*
A	2010	0.83	47	104	59	18.77	0.21
	2011	0.83	29	30	31	7.21	0.21
	2012	0.88	64	358	52	20.40	0.16
B	2010	0.79	46	218	69	19.45	0.24
	2011	0.75	27	113	56	12.76	0.23
	2012	0.71	52	291	63	23.32	0.19
C	2010	0.67	27	176	57	19.22	0.14
	2011	0.71	18	52	42	13.41	0.25
	2012	0.79	50	76	45	15.77	0.13
D	2010	0.83	31	77	42	16.88	0.08
	2011	0.75	37	29	26	14.11	0.14
	2012	0.75	36	208	49	22.38	0.08
E	2010	0.75	34	132	49	18.62	0.13
	2011	0.75	40	60	31	11.42	0.09
	2012	0.67	34	230	44	14.26	0.07
F	2010	0.50	12	89	50	17.16	0.17
	2011	0.50	17	34	26	3.36	0.11
	2012	0.71	45	215	43	14.91	0.11

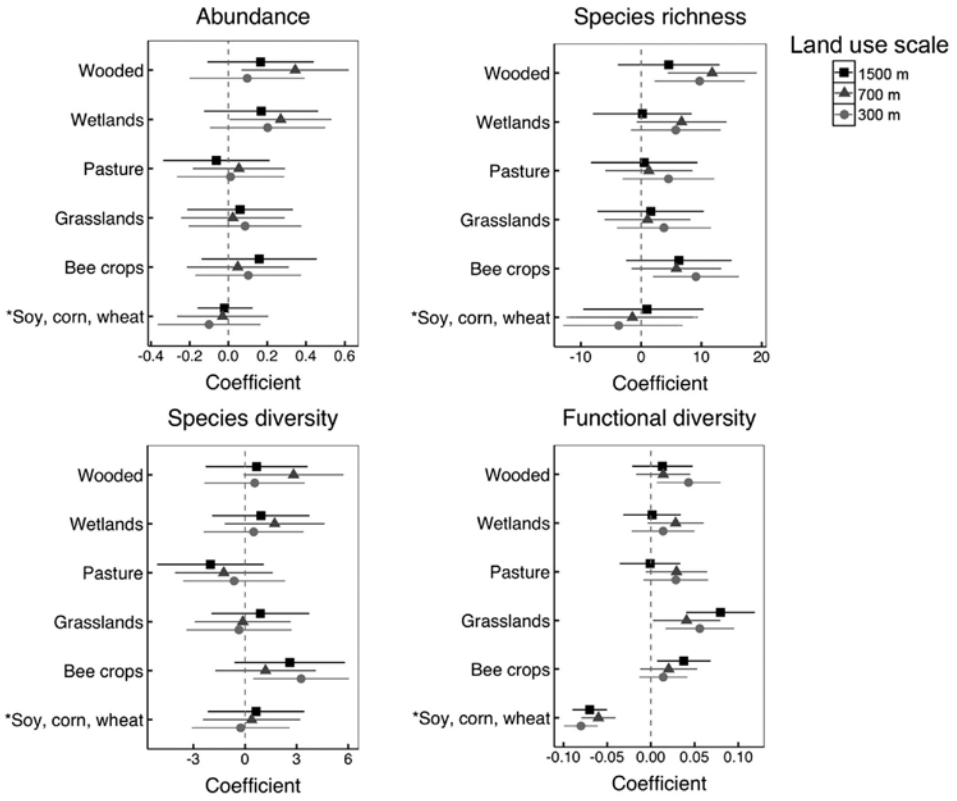

Fig. 3. Bee community measures and land use. Coefficients of fixed effect variables with 95% confidence intervals (CI) from mixed-effect models with proportion of land use at varying distances from collection locations. Effects of land use variables are significant when the 95% CI does not cross zero (e.g. abundance of bees in wooded areas and wetlands at 700m). All models are presented as standardized z-scores. *Separate single-effect models were constructed for the land use soy, corn, wheat.

the 3200m scale (β = -0.08, *CI*= -0.15 to -0.01), but no significant association at other scales (2000m: β = -0.08, *CI*= -0.16–0.00; 1000m: β = -0.07, *CI*= -0.15–0.02; 500m: β = -0.07, *CI*= -0.16–0.03), and no associations of these crops with honey production (3200m: β = -6.43, *CI*= -13.26–0.40; 2000m:, β = -6.06, *CI*= -14.14–2.02; 1000m: β = -4.64, *CI*= -13.27–3.99; 500m: β = -4.39, *CI*= -13.80–5.02).

4. Discussion

Our study demonstrates positive correlations between the success of wild bee communities and honey bee colonies embedded within an intensive agroecosystem. This finding suggests that habitat conservation, establishment,

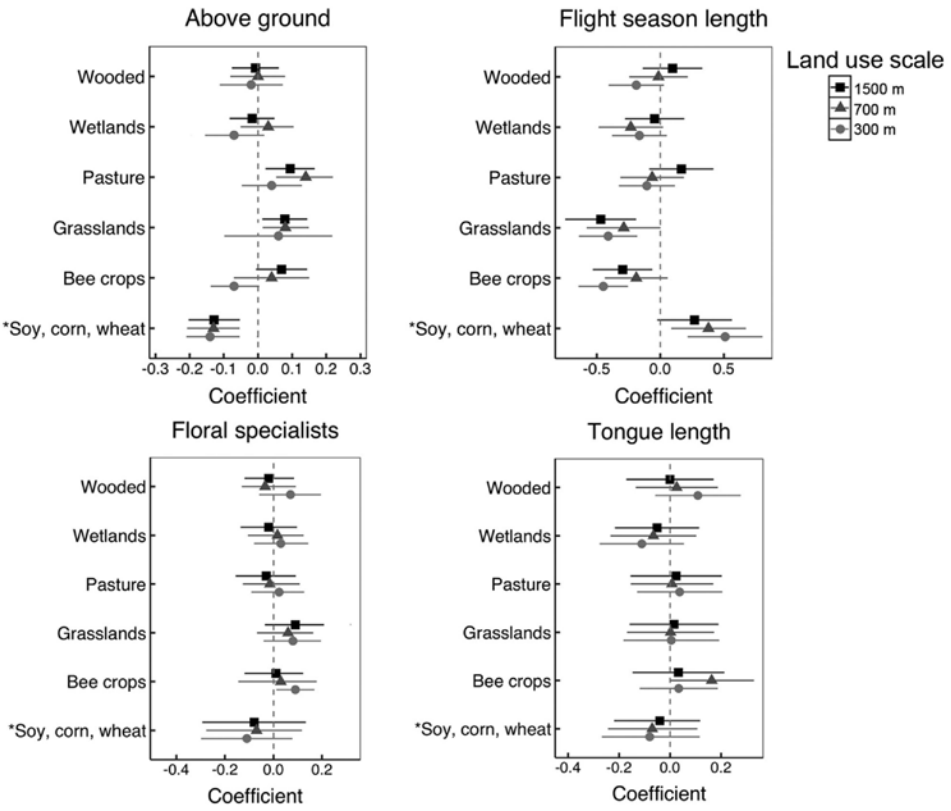

Fig. 4. Bee functional traits and land use. Coefficients of fixed effect variables with 95% confidence intervals (CI) from mixed-effect models with proportion of land use at varying distances from collection locations. Effects of land use are considered significant when the 95% CI does not cross zero (e.g. above ground nesting bees in grasslands and pasture at 1500m and 700m). All models are presented as standardized z-scores.
*Separate single-effect models were constructed for the land use soy, corn, wheat.

and enhancement in agricultural areas has the potential to support both pollinator groups at shared locations. Abundant floral resources required by honey bee colonies may also act to increase abundance and species diversity of wild bee communities. Conversely, we found a lack of a correlation between honey bee colony survival and wild bee success which could have been due to beekeeper management interventions (e.g. providing supplemental feed to colonies at various times of the year), thus increasing survival of honey bee colonies, even at poorer sites. In contrast, wild bee communities were more susceptible to potential negative effects of limited environmentally- available forage.

Land uses positively associated with higher metrics for wild bees— bee-forage crops, pasture, and grasslands — were often important sources of floral resources. A relatively small amount of bee-forage crops (approximately

16–160 hectares within 3200m) including sunflower (*Helianthus annuus*), canola (*Brassica rapa*), and alfalfa (*Medicago sativa*) positively affected wild bee communities. The effect was strongest within 300m, meaning wild bees benefited most when those crops were in close proximity, presumably within the foraging range of most of the bees. Despite relatively high floral cover (9%), pasture was not associated with a greater abundance of bees. Further study is needed to clarify the impact of pasture, including the impact of different grazing regimes on bee communities. The positive association of bees with shorter active seasons with grasslands could be due to a higher chance of synchrony with key floral resources found growing in grassland habitats. While land uses rich in floral resources are of clear importance to both honey bees and wild bees, there are differences in how they use these resources. Honey bees may be more able to take advantage of sporadically distributed floral resources due to forager recruitment via dance language communication and their larger foraging range compared to many other wild bee species (Beekman and Ratnieks, 2000; Dornhaus et al., 2006; Seeley, 1995).

Crop diversification could help increase floral availability in agricultural areas. The predominant land use across study sites was cropland containing corn, soybean, and small grain crops such as wheat, oats, barley, rye, and sorghum. The variety of commodities grown by North Dakota producers has steadily declined over the past century, with a dramatic increase in acreage dedicated to corn and soybean since 2007 (Gascoigne et al., 2013). This follows a global trend of decreasing crop diversity over the last 50 years (Khoury et al., 2014). With bee-forage crops comprising as little as 1% of the landscape in our study, we still observed benefits to wild bee communities. As such, crop diversification to include bee-forage crops, even at a relatively small scale, could substantially benefit wild bees.

Nesting habitat could be an important resource to support wild bee communities but is irrelevant to honey bee success. Land uses with low amounts of bee forage such as wetlands and wooded areas were shown to support wild bee communities possibly due to providing undisturbed areas for nesting. Many wetlands in the study region were small in area and ephemeral, leading to creation of undisturbed ground-nesting habitat around the periphery of the wetlands. Despite their importance in supporting bee communities, wooded areas were uncommon in the study area (2% of overall land use). Wooded shelterbelts are in decline since many are remnants from soil conservation efforts of the 1930s and these aging shelterbelts are being removed and not replaced (Marttila-Losure, 2013). The proximity of the effect (within 700m) indicates that more benefit could be derived from having shelterbelts dispersed throughout the landscape. The positive influence on bee communities could become even greater if flowering shrubs are also planted (Hannon and Sisk, 2009). Increased nesting

site availability for above-ground nesting bees in grasslands is a possible explanation for their positive association. The positive association of increased acreage of pasture with greater proportions of above-ground nesting bees, but lack of association with any of the broader bee community measures, such as diversity and abundance, could be due to partially grazed stubble providing nesting resources for above-ground nesters. Retention and replacement wetlands, wooded areas, and pastures in intensive agricultural areas could help maintain bee diversity and bee abundance by providing nesting habitat.

Soy, corn, wheat, and other small grain crops, the predominant land uses across study sites, were associated with decreased functional diversity, particularly affecting above-ground nesting bees and bees with short active season durations, supporting previous research (Williams et al., 2010; De Palma et al., 2015). We also found these crops to be associated with decreased honey bee survival. This land use is unlikely to provide floral resources or nesting sites to support wild or managed bees.

While we found potential beneficial land uses in agricultural lands, there are concerns that should be addressed. Pesticide exposure risk should be considered as pollinator habitat is established in areas with widespread pesticide use (Hladik et al., 2016; Krupke et al., 2012; Mogren and Lundgren, 2016). Negative effects on wild bees from competition from honey bees is another potential risk to wild bees in agricultural areas where honey bees are present in high densities and floral resources may be limited (Butz Huryn, 1997; Evans et al., 2018; Goulson, 2003; Mallinger et al., 2017; Paini, 2004; Thomson, 2016). Although we did not examine competitive effects, we did see increased success of wild bees when bee-supporting land uses were present at locations shared with honey bees colonies. This finding indicates the potential value of forage and habitat near apiaries to wild bee communities despite potential competitive effects.

Beyond their impacts on wild bee communities and managed honey bee colonies, semi-natural habitats situated among agricultural lands are of key importance for supporting other wildlife species and promoting biodiversity (Fargione et al., 2009; Moonen and Bàrberi, 2008). For example, agricultural lands were shown to be essential to the success of recovery plans for severely declining monarch butterfly populations (Thogmartin et al., 2017). Additionally, the diversification of agricultural lands and establishment of areas dedicated to grassland and pollinator habitat can provide a suite of ecosystem service benefits in agro-ecosystems (e.g. Werling et al., 2014), including reductions of pest populations (Gardiner et al., 2009) improving soil and water quality by mitigating runoff (Wratten et al., 2012), reducing greenhouse gas emissions (Fargione et al., 2008), and protecting against soil erosion (Montgomery, 2007).

5. Conclusions

Similarity in responses of wild bee communities and managed honey bee colonies to land use indicates that habitat establishment and enhancement in agro-ecosystems can serve both groups of pollinators. Semi-natural lands associated with greater success of both honey bees and wild bees included areas rich in floral resources, such as grasslands, as well as areas with high-quality nesting habitat, such as wooded areas. The association of crops providing bee forage with species diversity and honey production demonstrated the potential for these crops to support both honey bees and wild bees amongst intensively cultivated agricultural lands.

Although the current bee communities present in agriculturallydominated landscapes are not likely to include the full range of historical diversity, these landscapes can house remnants of native bee populations that are in need of preservation, particularly in areas where agricultural conversion is relatively recent, such as the NGP where tracts of native prairie were more common as recently as the last quarter to half century (Otto et al., 2016; Wright and Wimberly, 2013). Pollinator habitat initiatives that focus on planting flowers as well as on the retention and enhancement of landscape features providing nesting sites are well suited to support a diversity of pollinators.

Acknowledgments — The authors would like to thank Ned Euliss, Jeff Pettis, the collaborating beekeeper Zac Browning, USGS technician Jordan Neau, and bee taxonomists John Ascher, Jason Gibbs, Sam Droege, Mike Arduser, Karen Wright, and Joel Gardner. This project was funded by a grant from USDA-NIFA (2010-65615-20631).

Appendix A. Supplementary data — Supplementary material follows the References.

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	1500m			700m			300m		
	Min %	Max %	Mean %	Min %	Max %	Mean %	Min %	Max%	Mean%
Floral cover	1	83	22	0	100	25	0	100	23
Wooded	0	5	2	0	11	2	0	26	4
Open water	0	22	4	0	30	4	0	4	5
Wetlands	0	22	5	0	18	4	0	29	24
Grasslands	0	65	18	0	92	22	0	90	5
Hay land	0	13	3	0	33	6	0	42	8
Pasture	0	67	12	0	83	7	0	9	2
Bee crops	0	23	7	0	39	1	0	41	1
Soy, corn, wheat	5	91	50	0	93	50	0	100	46
Ruderal	1	77	18	0	93	18	0	98	20

Table S1. Minimum, maximum, and mean percent cover of floral cover and land uses surrounding bee survey locations at 1500m, 700m, and 300m. Measures of floral cover and land use were summarized over the three years of the study and the 18 survey locations.

Family	Species	Abundance	Nesting	Floral specialization	Tongue (mm)	Season length (months)
And.	*Perdita octomaculata*	36 (36)	below	oligolectic	1.47	1
Api.	*Bombus griseocollis*	106 (78)	above	polylectic	8.73	5
	Bombus ternarius	50 (32)	below	polylectic	6.19	5
	Ceratina mikmaqi	285 (96)	above	polylectic	2.78	5
	Melissodes agilis	431 (50)	below	polylectic	5.00	5
	Melissodes trinodis	693 (187)	below	oligolectic	5.60	5
Coll.	*Hylaeus affinis* group	170 (111)	above	polylectic	0.95	5
	Hylaeus mesillae	97 (93)	above	polylectic	0.85	5
Hal.	*Agapostemon texanus*	284 (9)	below	polylectic	2.65	5
	Agapostemon virescens	289 (31)	below	polylectic	2.95	5
	Dufourea marginata	100 (35)	below	oligolectic	2.17	4
	Halictus confusus	1511 (153)	below	polylectic	1.87	5
	Halictus ligatus	58 (28)	below	polylectic	2.20	5
	Halictus rubicundus	106 (15)	below	polylectic	2.58	5
	Lasioglossum admirandum	507 (46)	below	polylectic	1.65	5
	Lasioglossum albipenne	1252 (116)	below	polylectic	1.85	5
	Lasioglossum cf. *ephialtum*	110 (17)	below	polylectic	1.52	5
	Lasioglossum cf. *novascotiae*	1765 (166)	below	polylectic	1.66	5
	Lasioglossum paraforbesii	426 (27)	below	polylectic	2.36	5
	Lasioglossum pruinosum	1569 (42)	below	polylectic	1.66	5
	Lasioglossum sagax	494 (53)	below	polylectic	1.57	5
	Lasioglossum semicaeruleum	1024 (153)	below	polylectic	1.59	5
	Lasioglossum zonulum	878 (13)	below	polylectic	2.73	5

Table S2. Functional traits of bees comprising 90% of total collection. And.=Andreinidae, Col.=Colletidae, Api.=Apidae, Hal.=Halictidae. Total abundances from bowl and sweep trap collections of the most frequently collected bee species followed by total from sweep netting in parentheses. Tongue length was the combined length of the tongue, glossa, and prementum. Season length was the number of months during which adults were active.

Response variable	Fixed effects	Random effects	Error distribution
abundance	land-use categories, years	survey location nested within site	negative binomial
species richness	land-use categories, years	survey location nested within site	normal
species diversity	land-use categories, years	survey location nested within site`	normal
functional diversity	land-use categories, years	survey location nested within site	normal
community-weighted means of below-ground nesting	land-use categories, years	survey location nested within site	normal
natural log (n+1) transformation of community-weighted means of above-ground nesting	land-use categories, years	survey location nested within site	normal
community-weighted means of active season length	land-use categories, years	survey location nested within site	normal
natural log (n+1) transformation of community-weighted means of floral specialization	land-use categories, years	survey location nested within site	normal
community-weighted means of tongue length	land-use categories, years	survey location nested within site	normal

Table S3. Summary of mixed-effects multiple linear regression models

Mixed-effects multiple linear regression models with normal error distributions were fit using lme4 version 1.1-9 (Bates et al., 2015). The model with a negative binomial error distribution was fit using a log link function with glmmADMB version 0.8.3.3 (Fournier et al., 2012; Skaug et al., 2016). Land-use categories were wooded areas, wetlands, grasslands, pasture, hay land, potential bee forage crop land, and other crop land (predominately soy, corn, wheat). Years were 2010, 2011, and 2012. We removed hay land, ruderal lands (predominantly fallow land and ditches), and open water from all models due to collinearity affecting significance and direction of effects. We also removed the land-use grouping soy, corn, and wheat from all due to collinearity with other land uses (pasture, grasslands, bee-forage crops, wooded areas). We ran simple linear regression models with the category soy, corn, and wheat included as the predictor to examine the effect of this predominant land use (see main text). We examined remaining land-use factors with correlation coefficients greater than 0.40 with leave-one-out model comparisons to confirm that collinearity did not affect the significance of effects.

	1500m		700m		300m	
Abundance	AIC=471.1		AIC=465.8		AIC=471.2	
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Wooded	0.17	-0.11 – 0.44	**0.34**	**0.07 – 0.62**	0.10	-0.20 – 0.39
Wetlands	0.17	-0.13 – 0.46	**0.27**	**0.01 – 0.53**	0.20	-0.10 – 0.50
Pasture	-0.06	-0.34 – 0.21	0.05	-0.18 – 0.29	0.01	-0.27 – 0.29
Grasslands	0.06	-0.21 – 0.33	0.02	-0.24 – 0.29	0.09	-0.21 – 0.38
Bee crops	0.16	-0.14 – 0.46	0.05	-0.21 – 0.31	0.10	-0.17 – 0.37
	AIC=571.8		AIC=571.8		AIC=571.3	
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Soy, corn & wheat	-0.02	-0.15 - 0.12	-0.03	-0.28 – 0.22	-0.10	-0.36 – 0.17
Est species rich	R^2_{marg}=0.07	R^2_{cond}=0.25	R^2_{marg}=0.22	R^2_{cond}=0.29	R^2_{marg}=0.24	R^2_{cond}=0.24
	ß	***CI***	***ß***	***ß***	***ß***	***CI***
Wooded	4.57	-3.87 – 13.02	**11.79**	**4.40 – 19.17**	**9.71**	**2.22 – 17.19**
Wetlands	0.19	-8.00 – 8.39	6.71	-0.72 – 14.15	5.74	-1.69 – 13.18
Pasture	0.50	-8.34 – 9.33	1.27	-5.99 – 8.54	4.53	-3.07 – 12.12
Grasslands	1.59	-7.22 – 10.41	1.06	-6.10 – 8.21	3.78	-4.05 – 11.60
Bee crops	6.25	-2.51 – 15.02	5.84	-1.61 – 13.28	**9.09**	**1.95 – 16.22**
	R^2_{marg}=0.04	R^2_{cond}=0.24	R^2_{marg}=0.04	R^2_{cond}=0.23	R^2_{marg} =0.06	R^2_{cond}=0.22
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Soy, corn & wheat	1.66	-7.55 – 10.87	-2.15	-11.36 – 7.06	-3.74	-12.81 – 5.33
Exp *H'*	R^2_{marg}=0.05	R^2_{cond}=0.07	R^2_{marg}=0.10	R^2_{cond}=0.10	R^2_{marg}=0.11	R^2_{cond}=0.11
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Wooded	0.80	-2.37 – 3.97	**3.15**	**0.06 – 6.25**	0.80	-2.30 – 3.91
Wetlands	0.59	-2.44 – 3.62	1.87	-1.24 – 4.98	0.56	-2.52 – 3.63
Pasture	-1.78	-5.10 – 1.55	-0.99	-4.03 – 2.05	-0.63	-3.78 – 2.51
Grasslands	0.93	-2.12 – 3.98	-0.17	-3.14 – 2.81	-0.23	-3.48 – 3.01
Bee crops	2.79	-0.67 – 6.25	1.06	-2.05 – 4.18	**3.61**	**0.65 – 6.56**
	R^2_{marg}=0.001	R^2_{cond}=0.02	R^2_{marg}=0.001		R^2_{marg}=0.001	R^2_{cond}=0.03
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Soy, corn & wheat	0.36	-2.64 – 3.36	0.35	-2.66 – 3.36	-0.28	-3.31 – 2.75
FDis	R^2_{marg}=0.34	R^2_{cond}=0.73	R^2_{marg}=0.19	R^2_{cond}=0.60	R^2_{marg}=0.19	R^2_{cond}=0.60
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Wooded	0.01	-0.02 – 0.05	0.01	-0.02 – 0.05	**0.04**	**0.01 – 0.08**
Wetlands	0.00	-0.03 – 0.03	0.03	-0.00 – 0.06	0.01	-0.02 – 0.05
Pasture	0.00	-0.04 – 0.03	0.03	-0.01 – 0.06	0.03	-0.01 – 0.07
Grasslands	**0.08**	**0.04 – 0.12**	**0.04**	**0.00 – 0.08**	**0.06**	**0.02 – 0.10**
Bee crops	**0.04**	**0.01 – 0.07**	0.02	-0.01 – 0.05	0.01	-0.01 – 0.04
	R^2_{marg}=0.31	R^2_{cond}=0.68	R^2_{marg}=0.29	R^2_{cond}=0.68	R^2_{marg}=0.39	R^2_{cond}=0.69
	ß	***CI***	***ß***	***CI***	***ß***	***CI***
Soy, corn & wheat	**-0.07**	**-0.09 – -0.05**	**-0.06**	**-0.08 – -0.04**	**-0.08**	**-0.10 – -0.06**

Table S4. Bee community measures and land use.

Estimates and 95% confidence intervals from generalized linear mixed effect models for effects of land use on bee community measures with land use surrounding survey locations at 1500m, 700m, and 300m. Models for "soy, corn & wheat" were run separately. All models are presented as standardized z-scores. Values in bold have 95% confidence intervals that do not include zero. Marginal and conditional R^2 values are provide for model evaluation for models run with normal-error distributions and AIC values are provided for models run with negative binomial error distributions.

	1500m		700m		300m	
Above-ground nesters	R^2_{marg}=0.31	R^2_{cond}=0.31	R^2_{marg}=0.29	R^2_{cond}=0.52	R^2_{marg}=0.2	R^2_{cond}=0.47
	β	***CI***	***β***	***CI***	***β***	***CI***
Wooded	-0.01	-0.08 – 0.06	0.00	-0.07 – 0.07	-0.02	-0.11 – 0.06
Wetlands	-0.02	-0.08 – 0.05	0.03	-0.04 – 0.10	-0.07	-0.15 – 0.01
Pasture	**0.09**	**0.02 – 0.17**	**0.14**	**0.06 – 0.21**	0.04	-0.04 – 0.12
Grasslands	**0.08**	**0.01 – 0.14**	**0.08**	**0.01 – 0.15**	0.06	-0.05 – 0.17
Bee crops	0.07	-0.01 – 0.14	0.04	-0.04 – 0.11	**-0.07**	**-0.14 – -0.00**
	R^2_{marg}=0.22	R^2_{cond}=0.37	R^2_{marg}=0.24	R^2_{cond}=0.36	R^2_{marg}=0.25	R^2_{cond}=0.36
	Estimate	***CI***	***Estimate***	***CI***	***Estimate***	***CI***
Soy, corn & wheat	**-0.13**	**-0.20 – -0.05**	**-0.13**	**-0.21 – -0.06**	**-0.14**	**-0.21 – -0.06**
Flight season duration	R^2_{mare}=0.27	R^2_{cond}=0.53	R^2_{marg}=0.23, R^2_{cond}=0.51		R^2_{mare}=0.43	R^2_{cond}=0.53
	β	***CI***	***β***	***CI***	***β***	***CI***
Wooded	0.10	-0.14 – 0.33	-0.01	-0.24 – 0.22	-0.19	-0.41 – 0.03
Wetlands	-0.04	-0.28 – 0.19	-0.23	-0.49 – 0.02	-0.16	-0.38 – 0.05
Pasture	0.17	-0.09 – 0.42	-0.06	-0.31 – 0.19	-0.11	-0.33 – 0.11
Grasslands	**-0.47**	**-0.75 – -0.19**	-0.29	-0.58 – 0.00	**-0.41**	**-0.64 – -0.18**
Bee crops	**-0.30**	**-0.53 – -0.06**	-0.19	-0.44 – 0.06	**-0.45**	**-0.64 – -0.25**
	R^2_{marg}=0.04	R^2_{cond}=0.20	R^2_{marg}=0.05	R^2_{cond}=0.19	R^2_{marg}=0.06	R^2_{cond}=0.18
	Estimate	***CI***	***β***	***CI***	***β***	***CI***
Soy, corn & wheat	0.27	-0.03 – 0.57	**0.38**	**0.08 – 0.68**	**0.51**	**0.23 – 0.79**
Floral specialists	R^2_{mare}=0.09	R^2_{cond}=0.26	R^2_{mare}=0.08	R^2_{cond}=0.23	R^2_{mare}=0.14	R^2_{cond}=0.25
	β	***CI***	***β***	***CI***	***β***	***CI***
Wooded	-0.02	-0.13 – 0.08	-0.03	-0.13 – 0.07	0.07	-0.04 – 0.17
Wetlands	-0.02	-0.12 – 0.09	0.01	-0.10 – 0.12	0.03	-0.07 – 0.13
Pasture	-0.03	-0.14 – 0.08	-0.01	-0.11 – 0.10	0.02	-0.08 – 0.13
Grasslands	0.09	-0.03 – 0.20	0.06	-0.06 – 0.17	0.08	-0.04 – 0.19
Bee crops	0.01	-0.09 – 0.12	0.03	-0.07 – 0.14	0.09	-0.00 – 0.19
	R^2_{marg}=0.05	R^2_{cond}=0.21	R^2_{marg}=0.05	R^2_{cond}=0.21	R^2_{marg}=0.07	R^2_{cond}=0.22
	β	***CI***	***β***	***CI***	***β***	***CI***
Soy, corn & wheat	-0.08	-0.28 – 0.11	-0.07	-0.24 – 0.09	-0.11	-0.29 – 0.07
Tongue length	R^2_{mare}=0.12	R^2_{cond}=0.27	R^2_{marg}=0.17	R^2_{cond}=0.29	R^2_{mare}=0.18	R^2_{cond}=0.30
	β	***CI***	***β***	***CI***	***β***	***CI***
Wooded	0.00	-0.17 – 0.17	0.03	-0.13 – 0.19	0.11	-0.06 – 0.28
Wetlands	-0.05	-0.22 – 0.11	-0.07	-0.23 – 0.10	-0.11	-0.28 – 0.05
Pasture	0.02	-0.16 – 0.20	0.01	-0.15 – 0.17	0.04	-0.13 – 0.20
Grasslands	0.02	-0.16 – 0.19	0.00	-0.17 – 0.17	0.00	-0.18 – 0.19
Bee crops	0.03	-0.15 – 0.21	0.16	-0.00 – 0.33	0.03	-0.12 – 0.19
	R^2_{marg}=0.11	R^2_{cond}=0.18	R^2_{marg}=0.17	R^2_{cond}=0.24	R^2_{marg}=0.11	R^2_{cond}=0.16
	β	***CI***	***β***	***CI***	***β***	***CI***
Soy, corn & wheat	-0.04	-0.20 – 0.13	-0.07	-0.24 – 0.10	-0.08	-0.25 – 0.09

Table S5. Bee functional traits and land use.

Estimates and 95% confidence intervals for effects of land use on the community weighted trait mean with land use surrounding survey sites at 1500m, 700m, and 300m from generalized linear mixed effect models. Models for "soy, corn & wheat" were run separately. Trait values for above-ground nesting bees and floral specialists were log transformed. All models are presented as standardized z-scores. Values in bold have 95% confidence intervals that do not include zero. Marginal and conditional R^2 values are provide for model evaluation.